THE DAMSELFLY COMPOUND EYE IN THE STREAM HABITAT: BIOLOGICAL DESIGN FOR OBJECT DETECTION IN A DARK COMPLEX HABITAT

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Habitats characterized by high spatial variation in absolute light levels and spectral quality present a challenge to animals that rely on visual orientation and visual target discrimination. Insects, in particular, face several difficulties in visual performance related to the small absolute size and simplicity of visual components comprising their compound eyes, including the lack of a focusing mechanism, relatively limited light capture and course spatial resolution. Therefore, an understanding of the morphological and behavioral means by which insects overcome these limitations in order to perform highly demanding visual tasks can provide insight into both ecological specialization and artificial visual system optimization. We investigated optical geometry, perch orientation and microhabitat selection in the Hawaiian damselfly *Megalagrion xanthomelas*, a sit-and-wait predator that intercepts aerial prey among heterogeneous vegetation bordering streams and wetlands. We found that while the eyes of *Megalagrion xanthomelas* are roughly spherical, maximum visual acuity appears concentrated in an oblong region shifted below the equatorial frontal plane. This optical geometry corresponds well with typical orientations of damselflies resting on perches and suggests an arrangement maximizing detection of prey or conspecifics traveling along stream margins. We discuss the visual morphology and behavior of *Megalagrion xanthomelas* in relation to available light environments and in comparison to the visual systems of other species.

1   INTRODUCTION

How animals are able to detect targets of interest from a complex visual environment remains a critical question in visual physiology, functional morphology, and biomimetics (Horridge and Loughuet-Higgins, 1992). Insects, in particular, would seem to have several factors working against proficiency in visual discrimination tasks. In contrast to the mammalian visual system, insects have compound eyes rigidly fixed to their heads with minimal separation between the two eyes and no focusing mechanism (Land, 1997). Nevertheless, aerial insect predators rely on an ability to discriminate, pursue and intercept small and sometimes rapidly moving targets in visually cluttered three-dimensional environments of varied illumination. A primary constraint on insect vision and the capacity to perform these tasks is the typically coarse overall spatial resolution imposed by the necessarily small absolute size of the eyes (Land, 1997, 1989; Land and Nilsson, 2002). Compound eye resolution is limited by the number of individual lens facets and associated sensory units or ommatidia that can be fit to view a particular region of the visual field (Land and Nilsson, 2002). However, both optical quality (lack of diffraction blur) and light sensitivity decrease as facet diameter is reduced (Land, 1997) so that a trade-off arises if facets are arranged in symmetrical array on an eye of uniform surface curvature.

Typically, however, compound eyes are not uniform in interommatidial angle or facet diameter, so that sensitivity and visual acuity vary regionally across the eye (Land, 1989). Such patterns of regionalization can suggest details of an animal's ecology and selective pressures on its visual system (Horridge, 1978; Corbet, 1999). Conversely, examination of regionalization and visual specialization in animals with known ecology and behavioral patterns can provide important insight into the optimization of artificial visual systems engineered toward specific objectives with parallels in the natural world. Several well-defined general patterns of visual regionalization have been described and related to specific animal ecologies. For example, acute regions ("foveas") of reduced interommatidial angle, increased facet diameter or both appear as equatorial bands in the compound eyes of sand flat crabs, desert ants, and water-striders, all animals for which biologically relevant visual stimuli and locomotory trajectories occur within a vertically constricted region aligned with the horizon (Land, 1997). Flying insects, and particularly aerial predators, perform complex maneuvers in fully three-dimensional environments and can exhibit more varied patterns of regional acuity adapted to complement their behavior. Many dragonfly species both locate and pursue prey in flight and have separate acute zones oriented for prey scanning and forward flight (Labhart and Nilsson, 1995). Dragonflies of the family Aeshnidae that live in deserts, where the landscape horizon is seldom obstructed, have acute

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zones that run from from the horizontal meridian of one eye to the other, but those that live in coniferous forests, where the tops of trees usually obscure the horizon, have acute zones situated about 15°above the horizontal meridian (Corbet, 1999). Although much vision research has concerned dragonflies, particularly the large-eyed *Aeschna* and *Anax*species(Sherk, 1978), much less research has examined the related suborder of damselflies (Horridge, 1978).

Like dragonflies, damselflies are generalist aerial predators of insects in forested habitats along streams and ponds (Corbet, 1980). The distribution and spectral quality of light in forest riparian habitats can be quite complex as it is filtered through the canopy and reflected off a mosaic of disparate substrates including water, rocks, soil, and vegetation (Endler, 1993). It may also have some predictable heterogeneity, as we expect the light directly over the stream to be the least filtered by overhanging canopy and for some nearby sites to be heavily shaded from direct or even indirect solar illumination. Along with a generally more slender body form and lesser speed in flight, damselflies differ from dragonflies in more typically employing a repeated sit-and-wait predation strategy, perching until a prey item approaches and then flying to intercept the target (Polhemus and Asquith, 1996). This tactic of intermittent, stationary perching makes damselflies especially useful in research of potentially coadapted suites of morphological and behavioral traits by facilitating comparison of eye structure to fine-scale point selection of light microhabitats within a larger heterogeneous light environment.

In this study, we measured the light environment, perch site selection, orientation, and eye morphology of the damselfly species *Megalagrion xanthomelas*. We hypothesized that this species possesses both visual regionalization and nonrandom use of the available light environments consistent with maximization of light capture and concentration of visual acuity in specific fields of view. Because damselflies have predatory and locomotory patterns differing from those of the closely related dragonflies, description of damselfly visual morphology and behavior will allow for a more informative comparative examination of visual system specialization.

2   MATERIALS & METHODS

2.1   Study Site and Animals

M. xanthomelas is a small endemic Hawaiian damselfly species (adult length 33-37 mm) with sexually dimorphic coloration (Polhemus and Asquith, 1996). Measurements of light environments and perching characteristics of male *M. xanthomelas* were conducted along a stream at the Tripler Army Medical Center (TAMC) located on leeward Oahu (Honolulu, HI, USA). A detailed description of this location can be found elsewhere (Polhemus, 1996; Englund, 2001). The stream flows slowly below a narrow open corridor in an otherwise dense, mixed forest canopy. Damselflies alternate short flights with periods of perching on vegetation in the irregularly shaded stream margins (Polhemus and Asquith, 1996). While both sexes of *M. xanthomelas* are effective predators of small aerial prey, our study focused exclusively on males, which are territorial and appear more conspicuously in the riparian habitat. In Hawaii, damselflies do not appear to exhibit seasonal differences in behavior (Polhemus and Asquith, 1996). Our study was conducted from July 2007 to March 2008 between 9:30 and 14:00 local time on sunny days with little cloud cover (less than 30%). This sampling regime covers the main daily activity period of this species (Polhemus and Asquith, 1996).

2.2   Eye Morphology

Interommatidial angles of the left eyes of 5 male *M. xanthomelas* were measured according to the pseudopupil technique (Horridge, 1978; Land, 1997; Rutowski and Warrant, 2002) using isolated heads mounted on a Leitz goniometer (Wetzlar, Germany) and viewed with orthodromic illumination under magnification of dissecting light microscope. The pseudopupil is a dark region appearing in a compound eye to a viewer of that eye due to the absorption of photons by ommatidia imaging the viewer within the compound eye (Stavenga, 1979). The apparent relative size of the pseudopupil when viewed at a particular angle indicates the relative number of ommatidia directed at that angle. As a corollary to this, interommatidial angles can be determined as the ratio of degrees through which the eye is rotated to the number of facets over which the pseudopupil appears to move during that rotation (Stavenga, 1979). Rotating the mounted head in uniform angular steps

while taking digital photographs through the microscope objective, we mapped interommatidial angles along both a 90°latitudinal (anterior-lateral) and a 180°longitudinal (dorso-ventral) transect. The 0°point of both these transects was the anterior-most medial equatorial point of the eye so that the dorsal and lateral endpoints of the transects each occurred at 90°. We measured facet diameters via microscopy along these same transects as an indication of ommatidial light capture potential and, therefore, regionalization of light sensitivity. We calculated the maximum resolution as the reciprocal of twice the interommatidial angle (Land, 1997).

2.3 Perch Orientation and Incident Light

Upon observation of each of 100 damselflies in the field, perch orientation, including angle above the horizon and angle relative to the stream corridor, was recorded. Immediately following each of these orientation measurements, measurements were made of the light environment at the initial position of the damselfly. Light environments, including multidirectional irradiance and radiance, were measured with an Ocean Optics USB4000 portable spectroradiometer with a $400\,\mu m$ diameter fiber optic input. Irradiance, reported as an intensity in $\mu W\,cm^{-2}\,nm^{-2}$or a radiant flux in photons ($\mu mol\,m^{-2}\,s^{-1}\,nm^{-2}$), refers to the light impinging on a surface from a full hemisphere centered on the surface. Irradiance is typically associated with ambient light or downwelling solar illumination. Radiance, reported as an intensity per solid angle or steradian ($\mu W\,cm^{-2}\,nm^{-2}\,sr^{-1}$) or as a radiant flux in photons($\mu mol\,m^{-2}\,s^{-1}\,nm^{-2}\,sr^{-1}$), refers to the light emanating (usually via reflectance) from a source at a small acceptance angle. For each perch location we measured irradiance with a cosine-corrected irradiance probe pointing up at a right angle to the ground (up), parallel to the ground in the direction in which the damselfly was facing (forward), and directed laterally at right angles to the damselfly's long axis in line with each eye. The two lateral measurements were each classified as toward or away from both the sun and the stream corridor. Radiance measurements were taken in the same directions with a 4 degree acceptance angle radiance detector probe. Additionally, radiance measurements were taken in the direction of the angle (in both planes) that the damselfly was facing (fordam) and at the upward right angle to this direction (updam)(Fig 1).
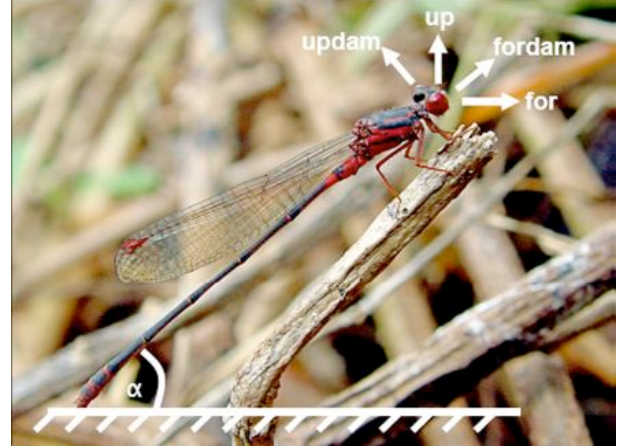

Figure 1: Probe orientations relative to the horizon for light measurements at a perching site of a male damselfly are defined as follows: for - parallel to the ground in forward direction, fordam - angle from abdomen to ground in forward direction, up - perpendicular to the ground, updam - assumed upward view of damselfly, perpendicular to fordam. Measurements were also taken with the probe perpendicular to fordam, in line with each of the eyes, and these were each designated as toward or away from the sun and toward and away from the stream.

2.4 Light Microhabitat Selection

In order to test for patterns of light microhabitat selection by damselflies we summarized variance in downwelling irradiance spectra at perches upon which damselflies were observed and at a random sample of 80 perches within the area of the study site through ordination by nonmetric multidimensional scaling (NMDS). NMDS is an ordination method with objectives and applications similar to those of principal components analysis and canonical correspondence analysis but without the restrictive assumption of linear relationships among variables (McCune and Grace, 2002). NMDS seeks by iterative search to arrange samples in the space defined by a specified number of dimensions so as to maintain the same ranked distances between samples in this ordination space as in the higher-dimensional space defined by the full set of original variables. Departure from monotonicity in the relationship between sample distances in the original and ordination spaces is reflected in a normalized stress value (Mather, 1976) scaled to range from 0 (perfect representation of the original distances in the reduced ordination space) to 1 (no representation of the original distances in the ordination space). The original irradiance spectra data for each perch site were

represented by mean intensities in 23 20nmbins. The NMDS analysis based on the lowest number of ordination axes producing a stress of less than 0.05 was taken as the best representation of the true dimensionality of the data. Kernel estimates of the distributions of selected and random perches in this ordination space were examined for separation and difference in shape.

3 RESULTS

Both facet diameter and interommatidial angle indicated heterogeneity in visual capability across the damselfly eye. Mean facet diameter ranged from 22.29 μm at the lateral margin of the eye to 34.47 μm in the central subequatorial region. Along the dorsoventral transect of the eye, facet diameter was greatest at between 5 and 15°below the equatorial frontal plane (Fig. 2). Longitudinally, along the anterior-lateral transect, facet diameter decreased from a maximum of 30.89 μm at the most forward oriented position to minima at an orientation near 90°. Interommatidial angles followed a similar pattern with minima at 0 and -5°along the longitudinal and latitudinal series respectively. Together these measurements indicate a single, high-acuity, high-sensitivity region directed forward and slightly downward. Figure 3 suggests the shape of this high-acuity region as imaged by the pseudopupil viewed from several angles. Viewed from the forward direction (Fig. 3), vertical elongation of the pseudopupil is apparent and indicates a higher number of ommatidia sampling a given vertical angle than sampling the same horizontal angle. Smaller pseudopupils visible from more lateral and dorsal positions (Fig. 3) indicate relatively reduced visual resolution in these directions. Our measurements indicate a maximum resolvable spatial frequency at the center of the high-acuity fovea of 0.72 cycles per degree (50 cycles per radian).

Damselflies perched at a mean angle of 29.2°(95% CI ±3.8°) above the horizon. Within the horizontal plane, damselflies perched at a mean angle of 116.0°(95% CI ±10.3°) from an orientation facing perpendicular to the stream corridor. The central tendency in the distribution of orientations was, therefore, that of a damselfly perching with the head facing at an an upward angle slightly away from the stream corridor although other orientations were quite common.

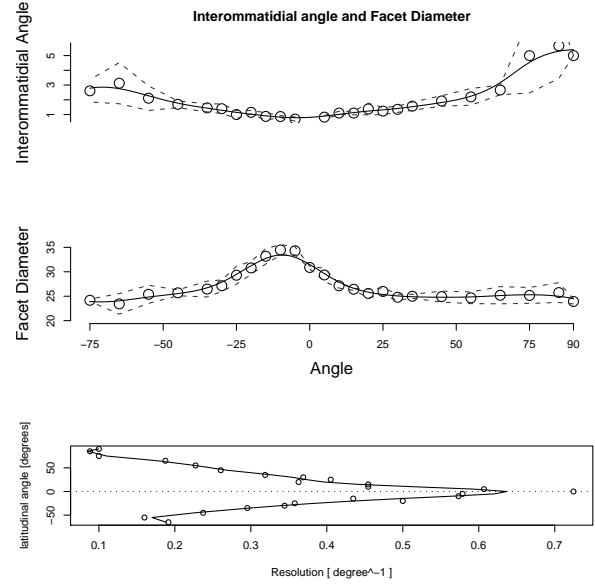Habitat light quality varied both in relation to the

Figure 2: Peaks indicating minimum interommatidial angle, maximum facet diameter, and maximum resolution are shown at between 0 and -15 °along the latitudinal transect of the damselfly eye.

open stream corridor and to sampled damselfly head orientations. At perch sites selected by damselflies downwelling irradiance from directly above (up) exceeded that measured in the horizontal orientation (forward) across all wavelengths (Fig. 4) and by an order of magnitude in the visible red regions of the spectra (approximately 620 to 700 nm). Peak irradiance of the downwelling spectra occurred at 680 nmwith an intensity of 10.323 μW cm^{-2} nm^{-2}or photon flux of 0.572 μmol m^{-2} s^{-1} nm^{-2}. Likewise, within the lateral orientation, the eye directed toward the sun viewed a significantly higher irradiance across all wavelengths than that directed away from the sun (Fig. 4). Orientation relative to the stream corridor did not significantly affect measured irradiance.

In contrast, relative to the eye directed towards the stream the radiance spectra of the eye directed away from the stream included significantly greater reflected light in visible green, yellow and red wavelengths (Fig. 5). The radiance viewed in line with the forward orientation of the damselfly (fordam) was significantly less than that from directly above, but did not differ from the radiance viewed from a purely horizontal forward orientation. Within the typical insect visible wavelengths (300 to 650 nm) the fordam radiance peaked at approximately 640 nmwith an intensity of 0.038
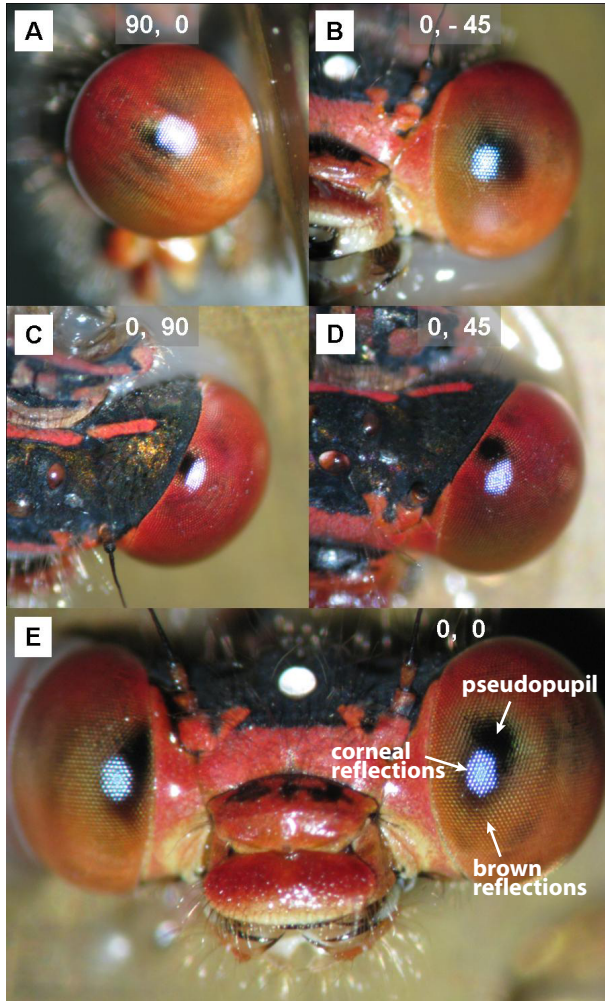
Figure 3: Photographs of the damselfly eye showing the pseudopupil as viewed from the latitudes and longitudes about the eye associated with the probe directions A) left , B) forward, C) updam, D) up, and E) fordam (only the eye at the right of the photograph is exactly aligned to the indicated latitude and longitude). The size of the black pseudopupil, indicating relative resolution, can be seen to vary according to viewing angle.
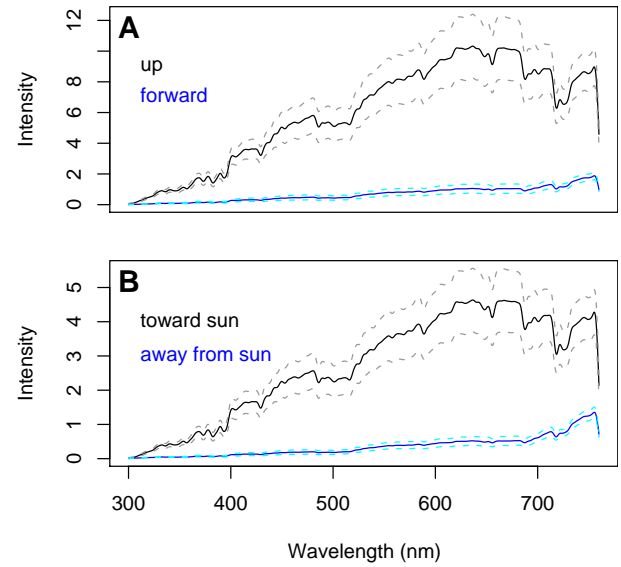

Figure 4: Irradiance intensity in $\mu\text{W cm}^{-2}\text{ nm}^{-2}$ at perch sites taken at the level of the damselfly eye. (A) Forward and up orientations (B) Irradiance lateral to the head, comparing the eye toward the sun versus away from the sun. Note that A and B are plotted over different ranges of intensity.

$\mu\text{W cm}^{-2}\text{ nm}^{-2}\text{ sr}^{-1}$ (0.002 $\mu\text{mol m}^{-2}\text{ s}^{-1}\text{ nm}^{-2}\text{ sr}^{-1}$). Total radiant photon flux in this direction was 0.274 $\mu\text{mol m}^{-2}\text{ s}^{-1}\text{ nm}^{-2}\text{ sr}^{-1}$. A flat, forward-facing area equal to that of a cross section through the largest damselfly facets would, therefore, receive approximately $1.27\,10^8$ photons s^{-1} within the visible wavelengths.

After standardizing downwelling irradiance relative to mean spectral intensity, variance in spectral quality among sites was found to be essentially one-dimensional (Fig. 6). Ordination by NMDS yielded a stress value of 0.04 indicating an excellent fit of the original multidimensional data to a single axis which was highly correlated with relative intensity of wavelengths between 400 nmand 700 nmand highly negatively correlated with relative intensity of wavelengths outside this range. This relationship indicates a pattern by which overall variance in habitat light quality is produced by relative intensity in the visible blue to near red wavelengths increasing most directly with total intensity so that spectra become increasingly hump-shaped at sites of greater downwelling irradiance. Damselfly discrimination of light habitats in this regard is suggested by a contrast between the strongly unimodal and positively positioned distribu-
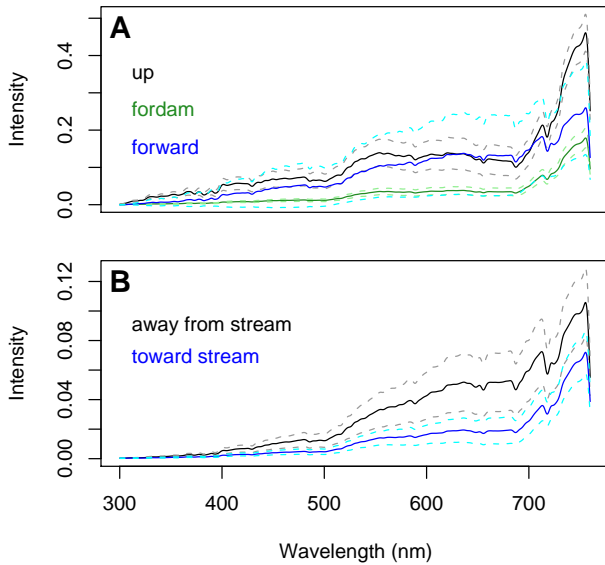
tion of selected perch sites and the broader, bimodal distribution of randomly sampled available perch sites along the NMDS axis. A correlated increase in total intensity and concavity of the spectral curve is apparent in a comparison of the irradiance spectra at the three modes, and is particularly striking between the high-intensity mode of the selected perch sites and the lower, low-intensity mode of the total available perch sites (Fig. 7).

Figure 5: Radiance intensity in $\mu W\,cm^{-2}\,nm^{-2}\,sr^{-1}$ at perch sites. taken at the level of the damselfly eye. Radiance measures the light at a small (4°solid angle) and is dominated by reflected light. (A) Comparison of forward, forward relative to the damselfly body axis (fordam), and upward (up) orientations. (B) Radiance lateral to the head, comparing the eye toward the stream versus away from the stream. Note that A and B are plotted over different ranges of intensity.
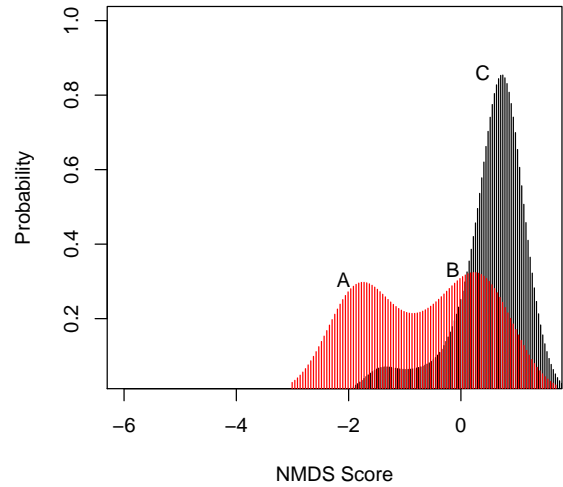

Figure 6: Estimated distributions of randomly sampled available perch site (red) and damselfly selected perch site (gray) NMDS scores differ in modality and position. The distribution of available perches has two clear modes (at A and B) whereas the distribution of perches selected by damselflies has a single strong mode (at C). The NMDS axis summarizes the shape of the downwelling irradiance spectrum and is highly correlated with total intensity of irradiance.

4   CONCLUSIONS

We found that while the eye of *M. xanthomelas* is roughly spherical, the ommatidia are regionalized so as to constitute a single conspicuous fovea. Interommatidial angles and facet diameters varied across the eye according to a similar pattern so that a forward oriented, and slightly ventrally shifted region contained both the narrowest interommatidial angles and the largest facets. These morphological findings correspond well with typical perch orientations. Damselflies tended to orient roughly parallel to or facing somewhat
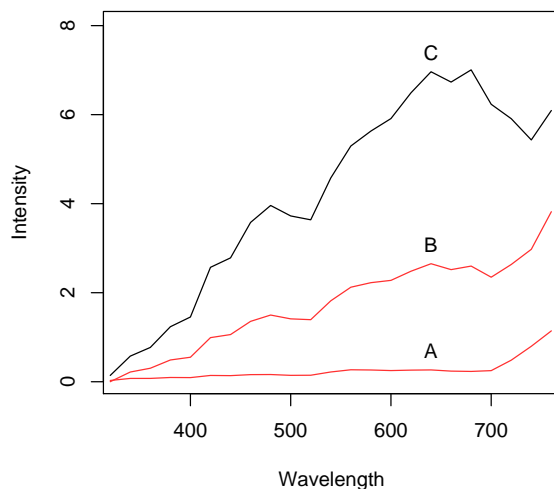
Figure 7: Downwelling irradiance (μW cm^{-2} nm^{-2}) spectra at the two modes (A and B) of the estimated distribution of randomly sampled available perch site NMDS scores and at the single mode (A) of the distribution of damselfly selected perch site NMDS scores

away from the stream in positions that could facilitate visual acquisition of prey items or conspecifics emerging from streamside vegetation and traveling along the stream corridor. Furthermore, the region of narrow interommatidial angles within the fovea was more elongate in the vertical than horizontal direction which would permit high forward visual acuity under a wide variety of perching angles. Additionally, the slightly ventral location of the point of maximum acuity on the eye would actually be oriented approximately 25 °above the horizon at the mean perching angle of the damselflies. Our results for the maximum resolvable spatial frequency in this high acuity region indicate that *M. xanthomelas* visual resolution exceeds that of most compound eyes despite the total diameter of the eye itself not exceeding 1.0 mm. Nevertheless, maximum resolution is only roughly half that of the largest eyes of *Aeschna* dragonflies and one hundredth that of the human eye (Land, 1981).

Although light environment heterogeneity is apparent in the damselfly habitat, there is some regularity that the damselflies appear to exploit on the level of microhabitat selection. Irradiance and radiance in the directions and at the vertical angles at which damselflies perched were generally not any greater than at an angle parallel to the horizon, despite the fact that irradiance and radiance were significantly higher in the full upward direction than in the forward direction. The particular sites at which damselflies were observed to perch did, however, differ from a random sample of available perch sites in downwelling irradiance, most conspicuously in total photon flux, especially in the longer wavelengths of the visible spectrum. This observation would be consistent with a hypothesis that all sites are not equal in regard to optimal visual performance and that some of the available light microhabitats would be limiting. It is interesting to note that the irradiance from the forward direction, even at selected sites, was relatively low and not significantly different from that in the direction of the lateral region of the eye oriented away from the sun. Thus, the high-acuity foveas tend to be in a rather dark environment. Although overall available light at selected perch sights and the morphology, size and position of the eyes suggest a potential visual field of nearly 360 °, relatively low radiance viewed by one or the other eye could limit the realized field of vision in some orientations. It appears, therefore, that the high competence of these animals in visual target acquisition is based on the combination of a a very broad, low-resolution field of vision coupled with narrow, forward oriented high-acuity regions that would be directed and function in unison. Subsequent research should examine initial prey pursuit trajectories of the damselflies in relation to the fine-scale distribution of visual units within the compound eye. Additionally, comparative study of visual morphology in others of the 16 species of *Megalagrion* damselflies would clarify the generality of these conclusions and indicate patterns by which similarly simple visual systems could be effectively adapted to a variety of specific conditions.

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